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RESEARCH PAPER

Plant communities and their environmental drivers on an arid mountain, Gebel Elba, Egypt

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Abstract

Aims: Gebel Elba is an arid mountain range supporting biological diversity that is incomparable to any other region of Egypt. This mountain has a vegetation structure and floristic community similar to the highlands of East Africa and the southwestern Arabian Peninsula. We aimed to provide the first classification of the vegetation units on Gebel Elba and identify the environmental factors controlling their distribution. **Study area:** Wadi Yahmib and its tributaries, which drain the north-western slopes of Gebel Elba, south-eastern Egypt. **Methods:** On the basis of 169 relevés, we used TWINSPAN to classify the perennial vegetation. We calculated separate GAMs for the deciduous and evergreen species to describe the patterns for each leaf strategy type with elevation. We used CCA to quantify the relationship between the perennial vegetation and the studied environmental factors. To estimate diversity and our sampling strategy, we used rarefaction curves for species richness. **Results:** We identified seven communities along the elevational gradient of Wadi Yahmib and its tributaries. We found that each community was restricted to a confined habitat depending on its drought resistance ability. Deciduous *Vachellia* woodland was the main vegetation type on Gebel Elba, while evergreen *Olea* woodland appeared in small fragments at higher elevations. We analysed the distribution patterns of deciduous and evergreen trees along the elevational gradient. We found a turnover at 500 m, indicating a potential ecotone between the *Vachellia* and *Olea* woodlands that was occupied by a *Ficus* community. CCA revealed the importance of altitude and soil quality in determining the vegetation structure of Gebel Elba. The species richness increased with elevation as a result of reduced stress and increased water availability at the upper wadis. **Conclusions:** This study identified seven vegetation units in the study area and showed the importance of orographic precipitation, soil quality and the complex topography in determining the habitats.

Taxonomic reference: Boulos (2009); names updated according to POWO (2019).

Abbreviations: CCA = Canonical Correspondence Analysis; GAM = Generalized Additive Model; TWINSPAN = Two Way Indicator Species Analysis.

Keywords

Acacia, Afromontane forest, classification, ecotone, Eritreo-Arabian, soil, vegetation, woodland

Introduction

The Eastern Desert of Egypt is characterized by coastal mountain ranges running parallel to the Red Sea. The most biodiverse mountain range in the region is the Gebel Elba in the south-eastern corner of Egypt, on the border between Egypt and Sudan (Kassas and Zahran 1971; Abd El-Ghani and Abdel-Khalik 2006). The flora of the Gebel Elba range is much richer than those of other coastal mountain ranges. In total, 458 plant species have been collected within the

area of Gebel Elba, representing almost 21% of the Egyptian flora (Boulos 2008; Zahran and Willis 2009). The other mountain ranges overlooking the Red Sea are less rich in plant diversity, with less than 130 species recorded in total (Zahran and Willis 2009). The proportion of Afrotropical elements on the Gebel Elba is much higher than those in any other region of Egypt (Abd El-Ghani and Abdel-Khalik 2006; Al-Gohary 2008). This range represents the northern limit of the Eritreo-Arabian province and the Sahel regional transition zone in Africa (Zohary 1973; White 1983), including the Somalia-Masai regional centre of endemism (White 1983; White and Léonard 1991; Boulos 2008). Thus, the Gebel Elba is considered one of the seven main phytogeographical regions of Egypt (Boulos 2009).

The biodiversity of the Gebel Elba region is unique to Egypt, and many globally threatened species are found there (IUCN 2019). In 1986 this area was declared the Gebel Elba National Park, covering nearly 36,000 km^2. Gebel Elba Mountain is the core part of this protected area. The richness of vegetation on Gebel Elba is related to its orographic precipitation. The proximity of Gebel Elba to the sea and its windward position create a unique ecosystem, known as a "mist oasis", that is found nowhere else in Egypt, but is comparable to similar ecosystems in Erkwit, Sudan, and the southern part of the Arabian Peninsula (Kassas 1956; Kürschner et al. 2004; Hegazy and Lovett-Doust 2016). Because of moisture-laden north-eastern winds, the vegetation is much richer on the northern slopes of Gebel Elba than on the southern slopes (Zahran and Willis 2009). Thus, both species richness and abundance are much higher on the mountain than in the exposed open desert (Abutaha et al. 2019). On the foothills of the mountain, *Vachellia tortilis* (synonym: *Acacia tortilis*) forms an extensive natural woodland landscape (Zahran and Willis 2009).

Gebel Elba has a unique phytogeographic position and a floristic composition that is more complex than the total floral composition of the rest of Egypt. This arid granite mountain bears floristic similarities and shares common vegetation with the neighbouring mountains of East Africa and the southwestern Arabian Peninsula (Kassas 1956; Hegazy et al. 1998). Gebel Elba and the southwestern Arabian highlands represent the northern limit of Eritreo-Arabian vegetation (Zohary 1973). The vegetation of the Eritreo-Arabian province is continuous and changes from deciduous *Vachellia-Commiphora* woodland at lower elevations to evergreen Afromontane forest of *Juniperus procera* at elevations above 2000 m (Zohary 1973; Kürschner et al. 2008; Deil 2014; Berhanu et al. 2018). The evergreen woodland dominated by *Olea europaea* subsp. *cuspidata* represents a transition zone between the lower montane *Vachellia-Commiphora* woodland and the upper montane *Juniperus procera* forest (White 1983; Kürschner et al. 2008). Comparably, Zohary (1973) recognized three altitudinal zones of Afrotropical vegetation in Gebel Elba: a lower zone of *Vachellia-Ziziphus* (pseudo-savanna vegetation), a middle zone of *Vachellia-Commiphora* (savanna vegetation), and a montane zone of *Olea-Ficus* forest fragments. Zahran and Willis (2009) found three altitudinal belts of vegetation on the northern slopes of Gebel Elba: a lower zone of *Euphorbia cuneata*, a middle zone of *E. nubica* and a higher zone of moist habitat vegetation. Within this higher zone, many evergreen species were recorded, such as *Euclea racemosa*, *Dodonaea viscosa*, *Carissa spinarum* and *Olea europaea* subsp. *cuspidata* (White 1983). The vegetation of Gebel Elba changes from *Vachellia tortilis* woodland at lower elevations to forested vegetation at middle and higher elevations (Abd El-Ghani and Abdel-Khalik 2006; Zahran and Willis 2009). The elevational gradient of Gebel Elba is known to harbour a relatively large number of tree species. Two prominent leaf strategy types occur (deciduous and evergreen). However, these types do not occur evenly across the elevational gradient; evergreen trees are prominent in the upper altitudes, while deciduous species are more common in the lower, arid parts of the gradient (Abutaha et al. 2019). The ecotone between evergreen woodland at higher elevations and deciduous woodland at lower elevations has not been studied (White 1983; Berhanu et al. 2018).

Most of the previous studies on Gebel Elba have mainly focused on wadis, which are temporary waterways that collect run-off water from the surrounding slopes and contain several microhabitats (Zohary 1973; Gomaa 2014), where vegetation is rich and continuous (Ahmed 1999; Zahran and Willis 2009; Abutaha et al. 2019). While the lower elevations of wadis show recognizable features of zonal communities, the vegetation on the higher slopes is more variable due to minor differences in habitat and recognizing clearly defined zonal communities is difficult (Zahran and Willis 2009). A classification of wadi vegetation is still lacking. Additionally, no agreement has been reached regarding the vegetation zonation of the northern wadis of Gebel Elba (Al-Gohary 2008; Zahran and Willis 2009). The altitudinal range of plant communities and information on environmental drivers are mostly unavailable. Thus, there is a need to identify the vegetation units of Gebel Elba and the environmental drivers controlling their distributions.

In this study, we aimed to describe the altitudinal zonation of the defined plant communities, their compositions and the relations to environmental factors in wadis on the northern slopes of Gebel Elba. This classification was based on 169 relevés which have not been previously sampled on this mountain. We also aimed to analyse the distribution patterns of deciduous and evergreen trees along the elevational gradient to identify a transition zone between the two different leaf strategy types representing different phytoregions. Finally, we also compared our findings on the diversity between the different vegetation communities with previous studies.

Materials and methods

Study area

Gebel Elba Mountain (1435 m) is located at 22.25N and ranges from 36.25 to 36.43E, nearly 15 km west of the Red

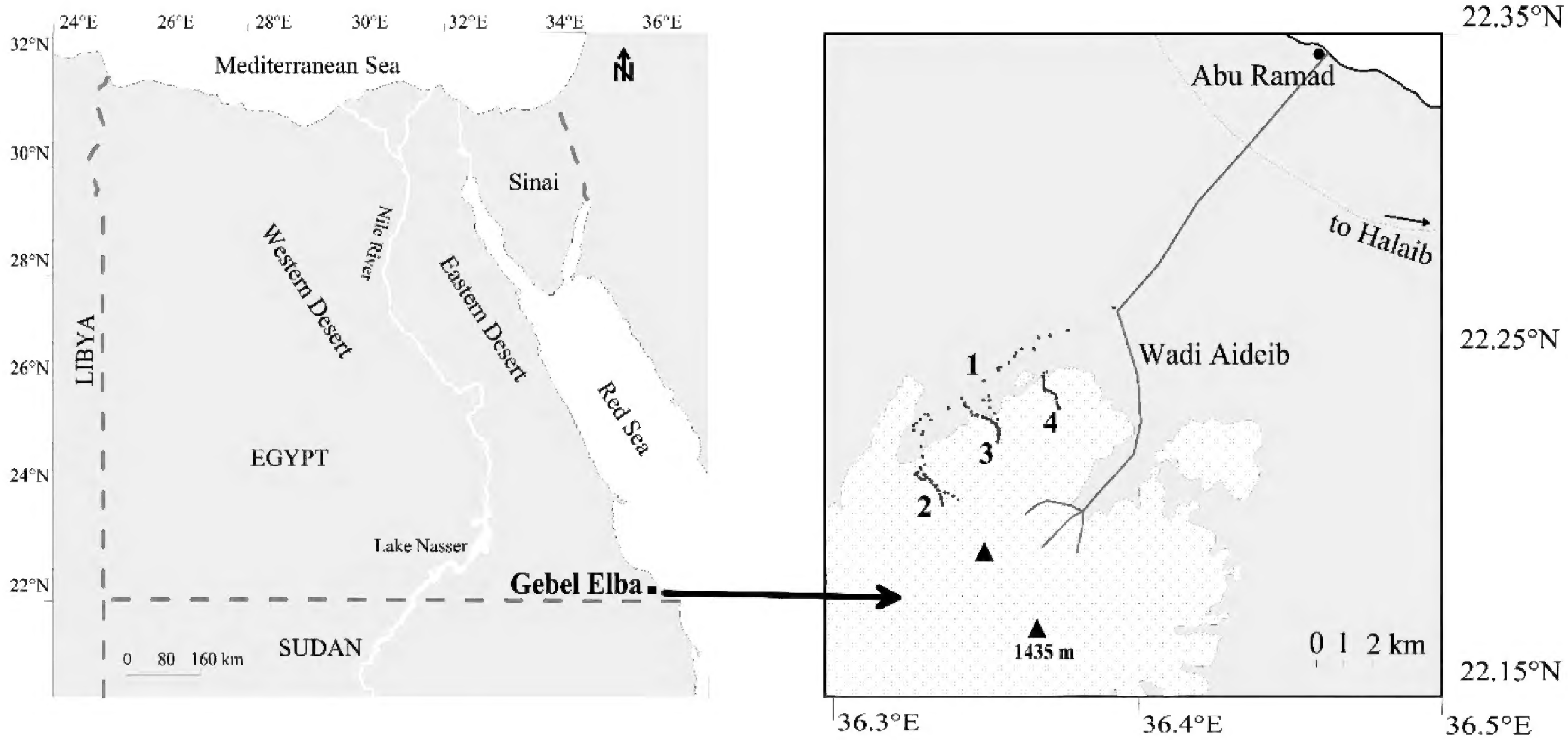

Figure 1. The location of Gebel Elba in Egypt (left) and the distribution of the vegetation relevés (green dots) surveyed for this study in Wadi Yahmib and its tributaries at the northern slopes of Gebel Elba (right); Wadi Yahmib (1), Wadi Marafai (2), Wadi Acow (3) and Wadi Kansisrob (4).

Sea coast, south-eastern Egypt (Figure 1). The mountain itself is formed of a group of granite peaks in the shape of a square with sides of approximately 15 km by 15 km. From the central peak, drainage lines (wadis) radiate in all directions (Ball 1912). The principal wadi on the northern slopes of Gebel Elba is Wadi Yahmib (Zahran and Willis 2009). Yahmib is located at the foothills of the mountain and receives water mainly from three mountainous tributaries: Wadis Marafai, Acow, and Kansisrob, which drain the western-northern flanks of Gebel Elba (Figure 1). The substrates of the wadis vary with an elevation gradient which increases from east to west; the substrate of Wadi Yahmib is fine sand, that of Wadi Kansisrob is coarse gravel, and Wadis Acow and Marafai, at higher elevations, have large granite boulder substrates (Abutaha et al. 2019).

Gebel Elba has a hyper-arid climate (Harris et al. 2014). The climatic aridity of the region is expressed in the climate diagram between 1985–2015 (Figure 2) adopted from Walter and Lieth (1967). The temperature ranges between 15.3 °C and 38.1 °C, with a mean annual temperature of 26.1 °C. The area received less than 40 mm of rainfall per year, mainly from winter rainfall and light summer rainfall (Figure 2). However, Gebel Elba receives up to 400 mm of orographic precipitation per year (Goodman and Meininger 1989; Kamel et al. 2015). Gebel Elba is influenced by winter rain and summer monsoons, dew falls regularly, clouds and mist shrouds the mountain (see Figure 5A–B). Although this mountain is surrounded by an extremely arid desert, orographic precipitation provides a climatic condition that is favourable for rich plant growth (Ball 1912; Hegazy and Lovett-Doust 2016).

Vegetation sampling

We conducted vegetation sampling on five visits; two in 2013, two in 2015 and one in 2016. The visits were made in January or March after the rainy season. We sampled 169 geo-referenced vegetation relevés that were marked with a GPS device (Garmin eTrex 30x). The relevés (10 m × 10 m) were distributed along transects in the four studied wadis, i.e., Yahmib, Marafai, Acow, and Kansisrob (see Abutaha et al. 2019). Locations of the relevés were selected randomly during the field work. For each relevé, we assembled a list of all vascular plant species that were present. We noted the growth forms of the listed species and identified the life forms according to Raunkiaer's system of classification (Raunkiaer 1934). Furthermore, we visually estimated the percentage cover of perennial species in each relevé. Owing to the arid climatic conditions of the study area, annual species were only noted as being present/absent. The nomenclature of the plant species followed Boulos (1999, 2000, 2002, 2005, 2009). We updated the list of taxonomic names according to Plants Of the World Online (POWO 2019) provided by the Royal Botanic Gardens, Kew. Voucher specimens were deposited in the Herbarium of Desert Research Center (CAIH) and the Herbarium Hamburgense (HBG).

Soil sampling and analysis

We took mixed soil samples from the surface layer (0–10 cm) of each relevé. We air-dried and analysed the samples to determine the physical and chemical soil properties. First, we determined soil texture by sieving with succes-

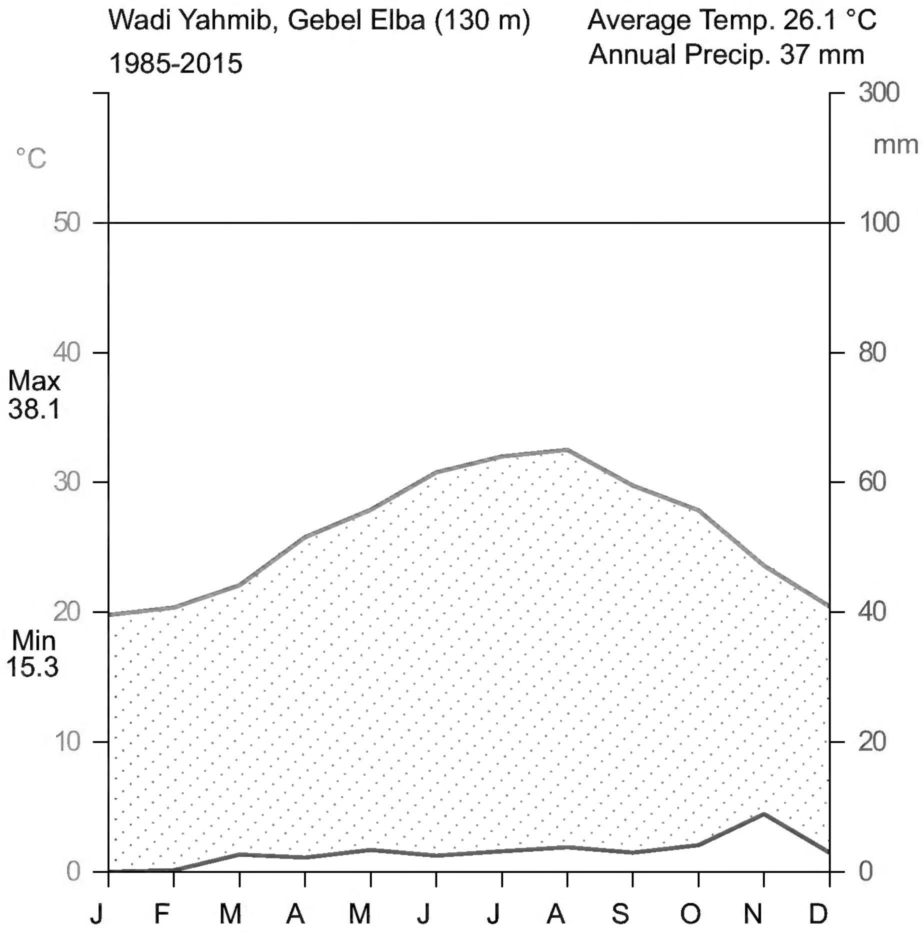

Figure 2. Climate diagram of Wadi Yahmib, Gebel Elba based on CRU datasets TS 4.01. Data is for the period from 1985 to 2015. The upper red line stands for mean monthly temperature of 26.1 °C (left axis); numbers beside the axis are the mean monthly maximum and minimum temperatures. The lower blue line stands for precipitation (right axis). Area shaded with dots (dotted area), above the precipitation line, and below the temperature line, indicates a dry period.

sively finer meshes (Estefan et al. 2013; AG Boden 2005). Second, we prepared soil suspensions by the addition of distilled water in a 1:1 ratio and stirring continuously for 2 hours, then measured the pH and electrical conductivity (EC) of the suspensions with a pH meter (Jenway 3510) and conductivity meter (Jenway 4510), respectively (Hendershot et al. 2008; Miller and Curtin 2008). We then filtered the soil suspensions and used the extracts to determine the soluble mineral contents. The analyses of major constituents in the soil extracts (calcium, magnesium, sodium, potassium, sulfate and chloride) were determined using an ion chromatography system, IC (Dionex, ICS-1100). Carbonate and bicarbonate ions were estimated with the titrimetric method (Jackson 1967; Estefan et al. 2013). Finally, we estimated the organic matter content by the weight loss-on-ignition method (Schulte and Hopkins 1996; Combs and Nathan 1998) and determined $CaCO_3$ volumetrically using a Collin's calcimeter (Piper 1950).

Data analysis
Multivariate analysis procedures

For the floristic classification of the relevés, we imported a vegetation matrix, including the percentage cover values of perennial species, into the software Juice, version 7.0 (Tichý 2002), and used the TWINSPAN classification (Hill 1979). We set the minimum group size to 3, and used percentage cover values of 0, 5 and 50 as cut levels. As a fidelity measure, we used the phi value (De Cáceres and Legendre 2009). The calculations of the phi values were adjusted for equal group sizes. If the phi value exceeded 0.25, a species was considered diagnostic, and if the phi value was > 0.50, the species was considered highly diagnostic; the p-value of Fisher's exact test was 0.05. Species with a frequency higher than 70% were considered as constant. To measure correlations between the perennial species and relevant environmental drivers, we used canonical correspondence analysis (CCA) for the ordination (Ter Braak and Prentice 1988). We selected altitude and edaphic factors after the exclusion of collinear variables (anions and cations were highly correlated with EC). We applied biplot scaling and the species were centred. Only perennials with significant phi values > 0.25 are shown in the ordination. We performed CCA using CANOCO, version 5.0 (Ter Braak and Šmilauer 2012).

To better describe and interpret the results of the classification, we used analysis of variance (ANOVA) and Tukey's post hoc tests for the pairwise comparisons to test for differences in the soil physical and chemical parameters between the identified plant communities. Before the statistical tests, each soil parameter was logarithmically or square root transformed in cases where the data did not follow a normal distribution. The analyses were carried out using R software (R Development Core Team 2018).

Diversity

To evaluate diversity and our sampling strategy, we used rarefaction and extrapolation sampling curves for species richness to estimate the completeness of our vegetation samples (Chao et al. 2014). We performed all calculations for the complete datasets (perennial and annual species) of the four wadis (transects) and for the identified plant communities. We constructed the rarefaction curves with the R-based interactive online programme *iNEXT* (Chao et al. 2016).

Distribution of deciduous and evergreen trees along the elevational gradient

We wanted to determine the altitude at which the change from deciduous to evergreen species occurred. To that end, we first classified each tree species as either deciduous or evergreen and determined the relative percentage of each leaf strategy type (LST) for the estimated plant cover per vegetation relevé along the elevation gradient from 130 to 680 m (14 relevés / 100 m). Then, we calculated separate generalized additive models (GAM) for each LST using the *mgcv* package (Wood 2017) with a binomial distribution and a cubic regression spline for elevation to model the relationship between the percentage of respective LST per relevé and elevation in metres. We plotted the respective models using the *ggplot2* package (Wickham 2016) in R 3.5.0 statistical software (R Development Core Team 2018).

Results

Floristic pattern

We recorded 162 vascular plant species (104 perennials and 58 annuals) belonging to 53 families (Appendix 1). The most common families were Fabaceae (9%), Poaceae (9%), Asteraceae (7%) and Malvaceae (7%). Poaceae is one of the species rich families in the study area. However, the grasses were less abundant (frequent) and were represented by many annual species (Appendix 1; Tables S1–S7 in Suppl. material 1). In total, 84% of the recorded species were found in the mountain tributaries feeding Wadi Yahmib. The number of species varied among the three tributaries: in Marafai, Acow and Kansisrob, there were 131, 99 and 76 species, respectively. The lowest number of plant species (n=26) were recorded in Wadi Yahmib itself, located in the open sandy plain. The dominant life forms were therophytes (36%), phanerophytes (27%) and chamaephytes (24%). Of all perennial species, 63% were woody species, including *Vachellia tortilis*, *Balanites aegyptiaca* and *Dodonaea viscosa*, while 37% were herbs, such as *Forsskaolea tenacissima*, *Cucumis prophetarum* and *Senna italica*. We recorded 21 tree species in Wadi Yahmib and its tributaries (Appendix 1).

Pattern of deciduous-evergreen trees

The response of the two LSTs, i.e., deciduous and evergreen, showed two clear decreasing and increasing patterns along the altitudinal gradient from 130 to 680 m (Figure 3). While there was a slight change below 400 m, the deciduous-evergreen ratio changed from 75/25 to 25/75 between 450 m and 600 m, indicating a potential ecotone; the switch between both LSTs was at 500 m. The smoothness of both GAMs was highly significant, demonstrating a clear pattern in the data. While there were very few evergreen species in the lower parts of the gradient (e.g., *Maerua crassifolia*), deciduous species did occur in low numbers at higher elevations, such as *Vachellia etbaica* (synonym: *Acacia etbaica*) and *V. tortilis*.

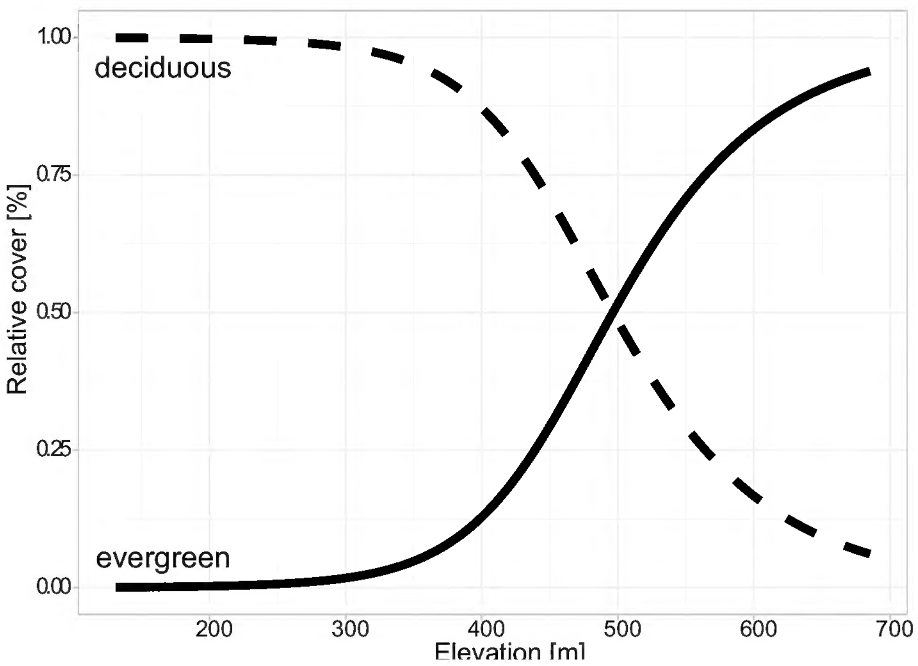

Figure 3. The relative proportions of deciduous and evergreen trees per vegetation relevé along the elevational gradient at the northern slopes of Gebel Elba. The pattern for deciduous tree species is shown as a dashed line while the evergreen tree species are represented by a solid line. The lines are the resulting smoothers of a cubic-regression GAM.

Classification

Seven woodland communities were described on Gebel Elba (Figure 4; Table 1). The first two communities (I-II) contained relevés from middle to higher elevations and were mainly composed of evergreens, while the communities (III-VII) in the lower part of the elevational gradient included relevés from low to middle elevations and were inhabited by deciduous trees (Tables 1, 2; Tables S1–S7 in Suppl. material 1). The observed communities were classified as follows.

I) *Dracaena ombet* – *Olea europaea* subsp. *cuspidata* community

This evergreen community was confined to the high elevations of Wadi Marafai, from 560 to 680 m. This community supported a high coverage of evergreen species and was characterized by six diagnostic evergreen species in total, including *Olea europaea* subsp. *cuspidata* and *Carissa spinarum* and two deciduous tree species, *Pistacia khinjuk* and *Vachellia etbaica*. The wadi bed was dominated mainly by *O. europaea* subsp. *cuspidata* (Figure 5C). The slopes were characterized by the growth of *V. etbaica* and *Dracaena ombet*. The vegetation in the wadi bed was dense and more vigorous than that occurring at lower elevations. In this community, many liana species, such as *Pergularia daemia*, *Jasminum fluminense* and *J. grandiflorum*, were climbing on olive trees. The soils of this community were often loamy sand on the side slopes and sandy loam in the wadi bed. The presence of large granite boulders increases water run-off to the main channels.

II) *Solanum incanum* – *Ficus salicifolia* community

This community was located mainly in moist habitats near flowing water or in the water courses of the high-elevation wadis, Wadis Acow and Marafai, at elevations from 346 to 550 m (Figure 5D). The vegetation consisted of two diagnostic fig trees (*Ficus salicifolia* and *F. palmata*) and two small shrubs (*Solanum incanum* and *Diceratella elliptica*). A characteristic species, *Searsia flexicaulis* (synonym: *Rhus flexicaulis*) from the former community, was also recorded in this community. The soil supporting this community was mainly loamy sand, and the organic matter content was the highest (0.41%, Table 3) of all seven communities. The organic matter content was related to the leaf litter of fig trees.

Table 1. Synoptic table of the seven communities showing percentage constancy values of the diagnostic species and non-diagnostic species with high constancy (> 70%). Diagnostic species are highlighted in light grey and highly diagnostic species in dark grey.

Community	I	II	III	IV	V	VI	VII
No. of plots	20	17	36	24	15	23	34
Total no. of species	80	73	84	84	48	68	72
Perennials	50	44	55	53	25	45	40
Annuals	30	29	29	31	23	23	32
No. of diagnostic species	8	4	1	1	2	3	2
***Dracaena ombet - Olea europaea* subsp. *cuspidata* community**							
Olea europaea subsp. *cuspidata*	90	12	-	-	-	-	-
Vachellia etbaica	45	-	-	-	-	4	-
Dracaena ombet subsp. *ombet*	40	-	3	-	-	-	-
Carissa spinarum	35	-	-	-	-	-	-
Searsia flexicaulis	55	35	-	-	-	-	-
Jasminum grandiflorum subsp. *floribundum*	30	-	-	-	-	-	-
Pistacia khinjuk var. *glabra*	30	6	-	-	-	-	-
Triumfetta flavescens	75	41	25	29	-	-	6
***Solanum incanum - Ficus salicifolia* community**							
Ficus salicifolia	10	47	14	-	-	-	-
Solanum incanum	55	76	17	-	7	-	15
Ficus palmata	-	18	-	-	-	-	-
Diceratella elliptica	-	18	3	-	-	-	-
***Vachellia tortilis* subsp. *tortilis* community**							
Vachellia tortilis subsp. *tortilis*	10	29	100	79	53	70	44
***Euphorbia nubica* community**							
Euphorbia nubica	-	-	17	88	33	57	24
Forsskaolea tenacissima	25	47	19	75	53	65	21
***Aerva javanica - Abutilon pannosum* community**							
Abutilon pannosum	-	24	8	8	100	48	9
Aerva javanica	-	18	11	4	67	35	6
Lycium shawii	-	18	50	50	73	39	26
***Euphorbia cuneata* community**							
Euphorbia cuneata	-	6	6	17	7	87	6
Tephrosia purpurea subsp. *apollinea*	-	-	11	67	87	83	26
Delonix elata	-	6	-	-	7	30	-
***Balanites aegyptiaca – Vachellia tortilis* subsp. *raddiana* community**							
Balanites aegyptiaca	-	-	11	38	13	-	85
Vachellia tortilis subsp. *raddiana*	-	-	3	8	13	9	44

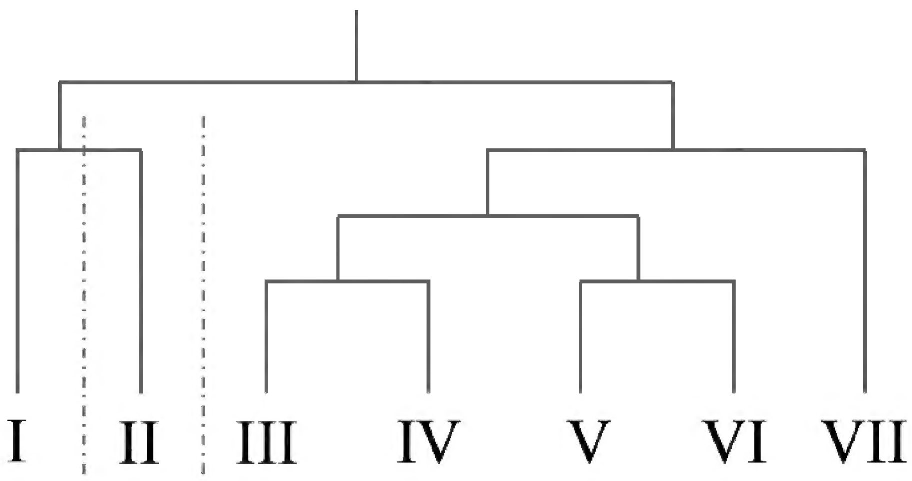

Figure 4. Dendrogram showing the TWINSPAN classification of the seven communities.

III) *Vachellia tortilis* subsp. *tortilis* community

This community was the most widespread one in the study area. The deciduous tree *Vachellia tortilis* subsp. *tortilis* was the only characteristic species (Figure 5E). This community occurred in a variety of habitats from low to middle elevations (130 to 383 m). The most common habitats of *V. tortilis* were the water channels of the wadis and gravelly terraces. This species was also abundant at the foot of Gebel Elba. The soil in this community was always sandy. The substrate deposits varied from fine sand in Wadi Yahmib to coarse sand deposits with gravel and rock detritus in the mountainous tributaries.

IV) *Euphorbia nubica* community

This community usually occurred on run-off slopes and the delta of Wadi Marafai. It was located in rocky habitats at middle elevations from 264 m to 379 m. The succulent shrub *Euphorbia nubica* was the only diagnostic species (Figure 5F). The tree layer was mainly absent on the run-off slopes, and *E. nubica* was the dominant succulent shrub, whereas *Forsskaolea tenacissima* grew on the lower run-off slopes of Wadi Kansisrob. Downward in the delta of Wadi Marafai, *E. nubica* grew in rocky outcrops between trees. We recorded the liana species *Cocculus pendulus* climbing on unhealthy trees of *Vachellia tortilis* and *Balanites aegyptiaca* in shady localities in the delta of Marafai. The soil texture was mainly loamy sand. This community had the highest silt (20.74%) and EC (1.59 mS/m) values.

V) *Aerva javanica – Abutilon pannosum* community

This community was located along the main channel of the tributary Wadi Kansisrob and occasionally downstream of

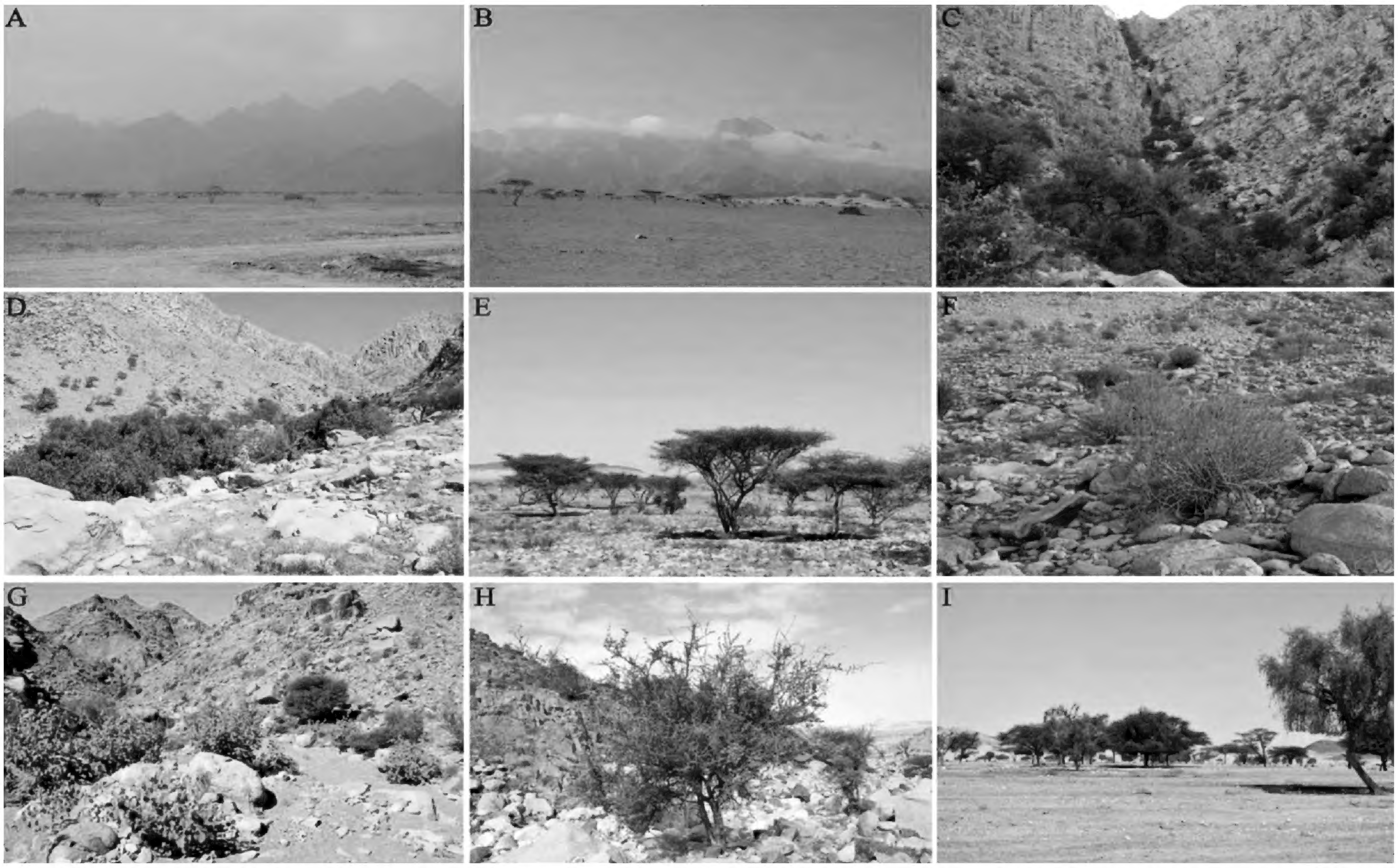

Figure 5. Representative photos showing Gebel Elba shrouded in mist (**A**) and clouds (**B**) accumulation on the Gebel Elba, and the leading species of the seven derived plant communities; *Olea europaea* subsp. *cuspidata* (**C**), *Ficus salicifolia* (**D**), *Vachellia tortilis* subsp. *tortilis* (**E**), *Euphorbia nubica* (**F**), *Abutilon pannosum* (**G**), *Euphorbia cuneata* (**H**), and *Balanites aegyptiaca* (**I**).

Table 2. Distribution of relevés, communities in the studied wadis, and the elevational gradients of the studied wadis and the seven communities (I–VII).

Communities		Localities				relevés per community
	Elevation	Yahmib (130–263 m)	Kansisrob (210–327 m)	Acow (228–410 m)	Marafai (350–680 m)	
I	(560–680 m)	–	–	–	20	20
II	(346–550 m)	–	–	9	8	17
III	(130–383 m)	11	1	16	8	36
IV	(264–379 m)	–	5	10	9	24
V	(237–275 m)	–	10	5	–	15
VI	(241–320 m)	–	17	6	–	23
VII	(196–361 m)	14	1	10	9	34
Total of relevés		25	34	56	54	169

Wadi Acow. It usually occurred in gravelly habitats near slopes at low elevations, from 237 to 275 m (Figure 5G). The two diagnostic species of this community were *Abutilon pannosum* and *Aerva javanica*. In this community, trees were less common, and the vegetation mainly consisted of shrubs and herbs, such as *Cucumis prophetarum*, *Tephrosia purpurea* and *Lycium shawii*. The soil was shallow, and the ground texture consisted of medium sand mixed with gravel and rock detritus. This community had the highest medium sand and pH values (38.46% and 7.73, respectively).

VI) *Euphorbia cuneata* community

This community occurred in the midstream areas of Wadi Kansisrob and was less frequent in Wadi Acow. It was often located in rocky habitats at elevations from 241 to 320 m (Figure 5H). Three diagnostic species characterized this community: two trees, *Euphorbia cuneata* and *Delonix elata*, and one herb, *Tephrosia purpurea*. The soil of this community had a high pH (7.63) and was similar to the soil of community V.

Table 3. Means and standard deviations for elevation and soil properties of the seven communities (I–VII). ANOVA test is for original, sqrt, or log data values, where values are not normally distributed. F-value and P-value refer to the ANOVA. Small letters denote the statistically different groups as identified by ANOVA post-hoc test.

	Parameter	I	II	III	IV	V	VI	VII	F-value	P-value
	Altitude.$_{log}$	^{a} 617.45 (57.72)	^{b} 450.49 (104.09)	^{c} 285.92 (96.63)	^{c} 321.51 (57.33)	^{c} 255.13 (19.43)	^{c} 280.51 (39.37)	^{c} 278.39 (82.94)	42.33	<0.001
Soil separates	Coarse sand.$_{sqrt}$	^{a} 22.88 (15.63)	^{ab} 14.25 (4.81)	^{b} 10.00 (7.09)	^{ab} 12.84 (4.94)	^{b} 11.13 (8.35)	^{ab} 15.48 (7.83)	^{ab} 14.39 (8.72)	5.073	<0.001
	Medium sand.$_{sqrt}$	^{bc} 27.75 (9.71)	^{abc} 32.80 (9.02)	^{ab} 36.10 (12.59)	^{c} 27.47 (8.06)	^{a} 38.46 (9.36)	^{a} 37.73 (8.64)	^{a} 37.92 (12.37)	4.997	<0.001
	Fine sand	^{b} 26.36 (10.58)	^{ab} 33.09 (5.46)	^{a} 37.76 (6.80)	^{a} 37.69 (6.12)	^{a} 36.78 (8.81)	^{ab} 32.82 (8.54)	^{ab} 32.88 (8.05)	5.997	<0.001
	Sand.$_{sqrt}$	^{b} 76.99 (15.41)	^{ab} 80.14 (9.33)	^{ab} 83.87 (9.39)	^{ab} 78.00 (7.80)	^{a} 86.37 (7.69)	^{a} 86.03 (7.49)	^{a} 85.19 (8.16)	3.823	<0.01
	Silt.$_{sqrt}$	^{ab} 20.06 (12.63)	^{ab} 18.75 (8.32)	^{ab} 15.28 (8.62)	^{a} 20.74 (6.86)	^{ab} 13.07 (7.31)	^{ab} 13.47 (7.18)	^{b} 14.04 (7.70)	2.968	<0.01
	Clay.$_{sqrt}$	^{a} 2.62 (3.27)	^{ab} 0.95 (1.20)	^{b} 0.77 (1.00)	^{ab} 1.21 (1.29)	^{b} 0.47 (0.57)	^{b} 0.36 (0.50)	^{b} 0.57 (0.91)	4.145	<0.001
Soil chemistry	pH	^{b} 7.26 (0.24)	^{b} 7.36 (0.24)	^{b} 7.35 (0.23)	^{b} 7.30 (0.20)	^{a} 7.73 (0.24)	^{a} 7.63 (0.26)	^{b} 7.26 (0.26)	12.41	<0.001
	EC$_{.log}$	^{c} 0.74 (0.35)	^{abc} 0.80 (0.20)	^{abc} 1.19 (0.98)	^{a} 1.59 (1.54)	^{bc} 0.84 (0.66)	^{abc} 1.12 (1.00)	^{ab} 1.20 (0.56)	4.199	<0.001
	$CaCO_{3.log}$	^{a} 1.05 (1.06)	^{ab} 1.21 (1.56)	^{c} 0.55 (0.39)	^{abc} 0.61 (0.31)	^{c} 0.54 (0.58)	^{abc} 0.71 (0.50)	^{bc} 0.57 (0.35)	4.096	<0.001
	$CO_{3.sqrt}$	^{a} 0.03 (0.02)	^{a} 0.04 (0.03)	^{a} 0.03 (0.01)	^{a} 0.04 (0.02)	^{a} 0.03 (0.02)	^{a} 0.03 (0.02)	^{a} 0.04 (0.04)	1.541	0.168
	$HCO_{3.log}$	^{b} 0.29 (0.17)	^{a} 0.63 (0.62)	^{ab} 0.35 (0.16)	^{a} 0.47 (0.20)	^{b} 0.24 (0.10)	^{b} 0.29 (0.14)	^{ab} 0.39 (0.19)	5.045	<0.001
	Organic matter.$_{sqrt}$	^{c} 0.11 (0.08)	^{a} 0.41 (0.30)	^{c} 0.20 (0.17)	^{ab} 0.35 (0.27)	^{c} 0.15 (0.12)	^{abc} 0.23 (0.16)	^{bc} 0.21 (0.19)	6.113	<0.001
	Ca.$_{log}$	^{b} 0.05 (0.02)	^{a} 0.09 (0.05)	^{a} 0.10 (0.08)	^{a} 0.14 (0.21)	^{ab} 0.07 (0.05)	^{ab} 0.08 (0.08)	^{a} 0.09 (0.05)	5.154	<0.001
	Mg.$_{log}$	^{b} 0.03 (0.02)	^{ab} 0.07 (0.07)	^{ab} 0.04 (0.02)	^{a} 0.06 (0.04)	^{b} 0.02 (0.01)	^{ab} 0.03 (0.02)	^{ab} 0.05 (0.03)	4.038	<0.001
	Na.$_{log}$	^{b} 0.04 (0.03)	^{ab} 0.04 (0.03)	^{a} 0.07 (0.05)	^{ab} 0.06 (0.06)	^{ab} 0.04 (0.04)	^{ab} 0.05 (0.05)	^{a} 0.06 (0.03)	3.652	<0.01
	K.$_{log}$	^{c} 0.04 (0.03)	^{ab} 0.09 (0.06)	^{ab} 0.09 (0.11)	^{a} 0.12 (0.11)	^{bc} 0.05 (0.05)	^{bc} 0.07 (0.10)	^{a} 0.09 (0.07)	7.485	<0.001
	SO_4	^{a} 0.02 (0.05)	^{a} 0.02 (0.02)	^{a} 0.08 (0.12)	^{a} 0.17 (0.55)	^{a} 0.08 (0.12)	^{a} 0.08 (0.14)	^{a} 0.07 (0.07)	1.06	0.389
	Cl.$_{log}$	^{c} 0.04 (0.04)	^{bc} 0.05 (0.05)	^{ab} 0.15 (0.20)	^{ab} 0.22 (0.43)	^{abc} 0.08 (0.13)	0.13 (0.20)	0.13 (0.10)	5.194	<0.001

VII) *Balanites aegyptiaca* – *Vachellia tortilis* subsp. *raddiana* community

This community was located in Wadi Yahmib and in the deltas of its tributaries at elevations ranging from 196 to 361 m. It was represented mainly by patches in Wadi Yahmib (Figure 5I) and some patches in the midstream areas of its tributaries. *Balanites aegyptiaca* and *Vachellia tortilis* subsp. *raddiana* were the two diagnostic species of this community. Unlike the *V. tortilis* subsp. *tortilis* community, which occurred in several habitats, this community was usually restricted to water channels. The soil supporting this community was usually pure sand with fine soil deposits.

Environmental drivers

The soils of the study area were characterized as neutral to slightly alkaline, with the mean pH value ranging from 7.26 to 7.73 (Table 3). The soil texture was pure sand on the desert plain and changed to sandy loam at higher elevations. The EC (0.74–1.59 mS/m) and mineral contents were low. The $CaCO_3$ content was less than 3% (0.54–1.21%), and the organic matter content ranged from 0.11 to 0.41% (Table 3), which is considered very low but typical for arid ecosystems.

The CCA results revealed that the edaphic factors changed with the elevational gradient (Figure 6). At the foot of Gebel Elba, the soil texture was defined primarily by fine and medium sands. High proportion of sands at low elevations led to poor water holding capacity, and thus, the EC of the surface layer increased. The vegetation in the sandy part of the gradient consisted mainly of deep-rooted tree species, e.g., *Vachellia tortilis* and *Balanites aegyptiaca*. At higher elevations on Gebel Elba, the silt and clay contents increased, thus supporting the growth of less drought-resistant species, such as *Ficus salicifolia*, *Olea europaea* subsp. *cuspidata*, *Carissa spinarum* and *Pistacia khinjuk* (Figure 6). Mountain communities at lower elevations, mainly in Wadi Kansisrob, contained plant species suited to higher soil pH values i.e., *Abutilon pannosum* and *Euphorbia cuneata*. Overall, Wadi Kansisrob was the driest and the least diverse among the studied mountainous wadis.

Plant diversity (species richness)

The plant diversity in the study area clearly differed between the four sampled wadis and the seven observed communities. Generally, Wadi Marafai was the most diverse wadi, with 131 species, while W. Yahmib was the least diverse, with only 26 species. When the sampling size was fixed at 24 relevés (Figure 7; Table 4), we expected the wadis to be ranked as Marafai > Acow > Kansisrob > Yahmib, which reflected the same order as the altitude gradient. The lower and upper bounds of the extrapolated species richness curve did not overlap, although there was some overlap between Acow and Kansisrob, yet there was still a significant difference in the lower bound of species richness (Figure 7; Table 4). Interestingly, these two wadis showed greater differences when the sampling rate was lower (Figure 7). When we compared the upper vs the lower bounds of species richness for the communities (Table 4), we recognized two main groups. The first group contained the communities with high species richness (I, II, and IV) from the higher wadis, i.e., Acow and Marafai. The communities located in the lower wadis, i.e., Kansisrob and Yahmib (III, V, VI, and VII) belonged to the second group, with significantly reduced species rich-

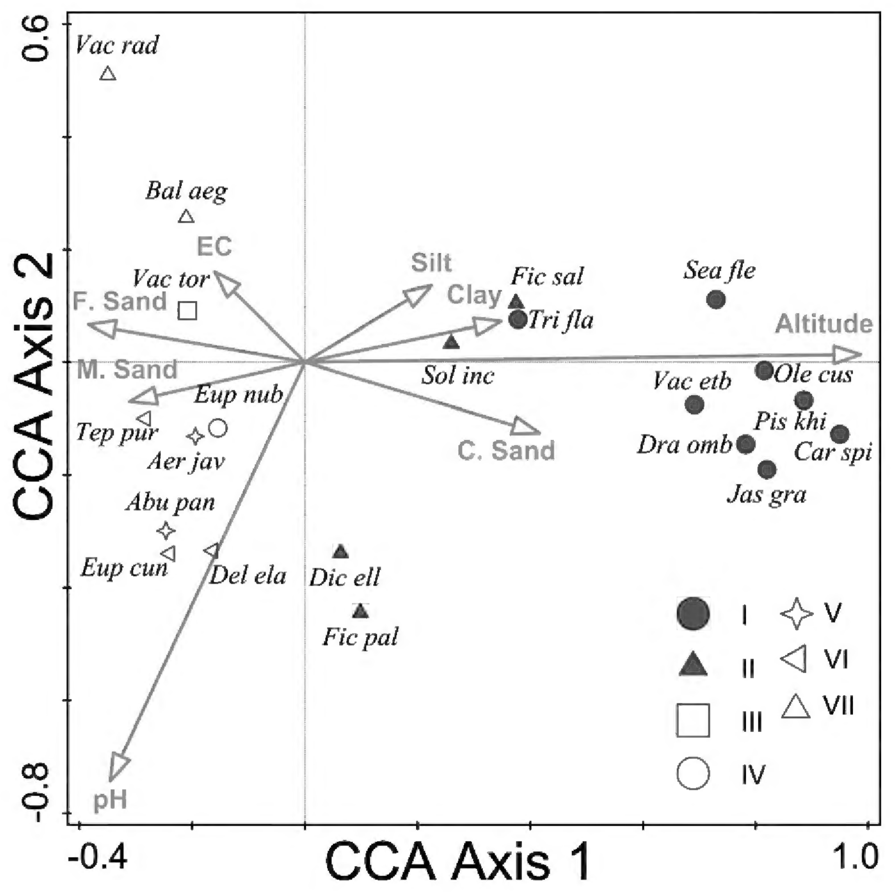

Figure 6. CCA ordination showing the relation between perennial species with phi coefficient > 0.25 and environmental factors represented by altitude and seven soil parameters. Variation is mostly explained by elevation (Alt), soil texture and pH. The lower left part contains species from Wadi Kansisrob. The upper part contains species of the open sandy plain, Wadi Yahmib. The right part contains evergreen species from mid to higher elevations. Eigenvalues for biplot scaling are 0.60 for axis 1 and 0.16 for axis 2 and the adjusted explained variation is 11.54%. The legend is placed at the lower right part of the figure. The diagnostic species for each community are represented by different symbols; solid symbols for communities of higher elevations and hollow symbols for communities from low to middle elevations. For species and sand fractions abbreviations see Tables 1, 3.

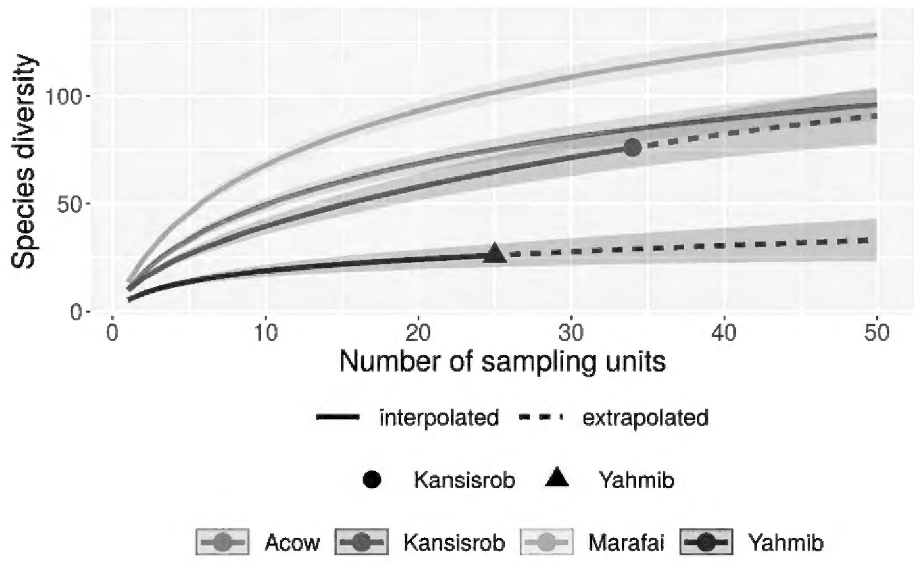

Figure 7. Sample-size-based rarefaction and extrapolation sampling curve for the four studied wadis.

Table 4. Sample based rarified richness for the four studied wadis and the seven studied communities at sample size equal 24 relevés for wadis and 13 for communities.

		t	Richness	Lower	upper
Wadi	**Marafai**	24	100.15	94.30	106.00
	Acow	24	74.02	69.65	78.38
	Kansisrob	24	63.62	56.94	70.30
	Yahmib	24	25.64	20.11	31.17
Community	**I**	13	68.11	62.97	73.25
	II	13	65.15	58.88	71.43
	III	13	52.35	47.51	57.20
	IV	13	63.73	57.82	69.64
	V	13	44.07	37.58	50.56
	VI	13	51.54	45.51	57.57
	VII	13	46.26	41.87	50.65

ness (significant because the upper confidence value did not overlap with the lower value of the other group).

Discussion

Floristic pattern

The location of Gebel Elba offers a lush "mist oasis" ecosystem where the sea-facing slopes are blanketed by moisture-laden clouds (Hegazy and Lovett-Doust 2016). Gebel Elba Mountain acts as a refuge for tropical flora in an otherwise arid regional climate. While the flora of Gebel Elba is found across south Egypt, the floristic composition is similar to that of neighbouring mountains, such as Jebel Marra, Sudan, and the Asir Mountains, Saudi Arabia (Wickens 1976; Hegazy et al. 1998). Fabaceae, Poaceae and Asteraceae have previously been reported as the most common families on Gebel Elba and in the arid mountains of East Africa and the southern Arabian Peninsula (Abd El-Ghani and Abdel-Khalik 2006). We found that therophytes, phanerophytes and chamaephytes were the dominant life forms in Gebel Elba. Similar results for life forms were observed in the Eastern desert of Egypt and in south-western Saudi Arabia (Abd El-Ghani and Abdel-Khalik 2006). The flora of East Africa and southwest Asia is influenced by Somalia-Masai elements. The Somalia-Masai regional centre of endemism is covered by deciduous and evergreen bushlands, while grasses are represented by a few annual and short-lived perennial species (White 1983; White and Léonard 1991). According to Zohary (1973), Gebel Elba and southwestern Arabia harbour Sudanian floras and represent the northern boundaries of the Eritreo-Arabian province. This area comprises a belt of savanna vegetation in East Africa and extends through tropical Arabia (Zohary 1973; Zahran and Willis 2009). The Sudanian flora of Gebel Elba is characterized by a large proportion of tropical shrub and tree species (Zohary 1973; Abd El-Ghani and Abdel-Khalik 2006; Al-Gohary 2008). The number of tree species we recorded (n=21) was greater than other studies found in similar regions in Egypt (e.g. Boulos 2008). The most abundant species were deciduous trees at lower elevations, e.g., *Vachellia tortilis* subsp. *tortilis*, *V. tortilis* subsp. *raddiana* and *Balanites aegyptiaca*, while evergreen trees characterized the higher elevations, such as *Searsia flexicaulis* and *Olea europaea* subsp. *cuspidata*. It is misleading to describe the vegetation as savanna depending on the floristic list only, because Gebel Elba is characterized by deciduous bushland and grasses contribute little to the plant biomass (White 1983).

Classification

Many Saharo-Arabian vegetation types grow in Egypt, and Sudanian vegetation is represented only in the southern part of Egypt. The Sudanian vegetation is divided into Nubo-Sindian vegetation, mainly in desert wadis and depressions, and Eritreo-Arabian vegetation, which is restricted to the Gebel Elba region (Zohary 1973). According to White and Léonard (1991) and Boulos (2008), vegetation of the Gebel Elba represents a satellite of the Somalia-Masai region, and the southern part of the Arabian Peninsula is an extension of this region into southwest Asia. However, Gebel Elba is lower than the tropical mountain ranges in the area (Ghazanfar 1991; Hegazy et al. 1998). The vegetation showed altitudinal zonation that was comparable to the patterns in East Africa and tropical Arabia. Two main climatic zones were observed, both of which are typical for East Africa and tropical Arabia. Palaeotropical *Vachellia-Commiphora* woodland was present from the foothills of Gebel Elba to the middle elevations, and the mist zone showed fragments of Afromontane forest dominated by *O. europaea* subsp. *cuspidata* (Zohary 1973; Zahran and Willis 2009).

Our classification results for the northern slopes of Gebel Elba accorded with the observation of Zahran and Willis (2009). According to Zohary (1973), the lower elevations of Gebel Elba were classified as Acacietea sudano-arabica. This class comprises the bulk of the xerotropical vegetation on Gebel Elba from low to middle elevations. In this study, we described six communities within deciduous *Vachellia-Commiphora* woodland and one community within evergreen *Olea* woodland. However, the fine resolution of this study allowed us to characterize specific habitats within each community, thereby providing a more exact zonation of the plant communities along the altitudinal gradients.

Only two communities represented the desert plains and foothills to the mid elevations of Gebel Elba, forming an open woodland; *Balanites aegyptiaca - Vachellia tortilis* subsp. *raddiana* and *Vachellia tortilis* subsp. *tortilis*, although the former was restricted to the main water channels. The *V. tortilis* subsp. *tortilis* community is more drought resistant and occurred in several habitats, e.g., channels, terraces and gentle slopes. *V. tortilis* subsp. *raddiana* is much more widespread in the Eastern Desert and Sinai Peninsula (Zohary 1973; Abutaha 2010; Morsy et al. 2010), whereas *V. tortilis* subsp. *tortilis* communities are mostly confined to the southern part of Egypt, Sudan and tropical Arabia (Kassas 1957; Ghazanfar 1991; Zahran and Willis 2009).

In the mountain wadis, the lower part of the elevation gradient (210–350 m) was more arid than the higher part (350–680 m). Three communities were recorded in rocky habitats (stony, rocky outcrops and run-off slopes) from low to middle elevations. Stony habitats near run-off slopes were occupied by *Aerva javanica – Abutilon pannosum* community. This community was characterized by frutescent vegetation. The characteristic species were shrubs and herbs, whereas the tree layer was less established. *Aerva* communities are more common in stony wadis and the southern slopes of Gebel Elba (Ahmed 1999; Zahran and Willis 2009). Additionally, *Aerva javanica* and *Abutilon pannosum* are frequent in the frutescent communities of the Hijaz Mountains, Saudi Arabia (Abd El-Ghani 1996). Rocky outcrop habitats are more favourable for plants than habitats with shallow soil containing stones in the upper layer, because rainwater can accumulate in rock crevices, leading to well-developed soil. In addition, rocks offer shade for herbs (Zohary 1973). We found that the *Euphorbia cuneata* community dominated this habitat in the lower parts of the northern slopes of Gebel Elba. While this community is found on the northern slopes of Gebel Elba and is common in the arid zones of Erkwit, the species *Euphorbia cuneata* has occasionally been recorded in the runnels of the southern slopes of Gebel Elba (Kassas 1956; Zahran and Willis 2009). At middle elevations, the succulent species, *Euphorbia nubica*, grows on run-off slopes and rocky outcrops. *Euphorbia cuneata* community is replaced by *Euphorbia nubica* community on rocky outcrops as the elevation increases. This distribution pattern of the two *Euphorbia* communities on Gebel Elba was comparable to that of the coastal mountains of Sudan (Kassas 1960; Zahran and Willis 2009). While rainwater is well preserved between boulders in wadi beds, run-off slopes are dry habitats, and rainfall is less available for plants (Deil 2014). Thus, the succulent *E. nubica* community is the pedoclimax community on the run-off slopes of Gebel Elba, whereas *Vachellia-Commiphora* woodland is the climax community on wadi beds. This distribution pattern is comparable to the pattern of succulent vegetation in Yemen; however, we did not record any similar communities (Deil 2014).

The higher elevations of Gebel Elba are influenced relatively by monsoon clouds more than the lowlands. The vegetation in this moist zone is less resistant to drought and is represented by fragments of *Ficus* and *Olea* forest (Zohary 1973). Similarly to Zohary, we identified two communities, *Solanum incanum - Ficus salicifolia* which is found lower down than *Dracaena ombet - Olea europaea* subsp. *cuspidata*; the former represents the *Ficus* community, whereas the latter represents the *Olea* community. *Ficus* is a typical wadi species that grows on water run-on habitats in *Vachellia-Commiphora* woodlands (Zohary 1973; Ghazanfar 1991). *Vachellia tortilis* subsp. *tortilis* is frequent in this community, which also contains characteristic species of *Olea* communities. In our view, this community represents an ecotone (transitional plant community) between the *Vachellia* and *Olea* woodlands.

Dracaena ombet - Olea europaea subsp. *cuspidata* was found in the mist zone of Gebel Elba. Many characteristic species from the evergreen *Olea* woodland can be observed here, such as *Dodonaea viscosa*, *Euclea racemosa* and *Maytenus senegalensis*. The wadi bed was dominated mainly by evergreen trees, such as *O. europaea* subsp. *cuspidata* and *Searsia flexicaulis*, which may form forest-like growth (Abd El-Ghani and Abdel-Khalik 2006). Plant individuals

were crowded in patches (Zahran and Willis 2009) due to the presence of many liana species on olive trees, such as *Pergularia daemia*, *Jasminum fluminense* and *J. grandiflorum*. The olive community contained many vascular species that are the least resistant to drought and are thus confined to the highest elevations of the northern slopes of Gebel Elba (Zahran and Willis 2009). The mountain slopes were characterized by rich *Vachellia etbaica* growth, which was also recorded on the northern slopes of three coastal mountains in the Elba range but not on the inland mountains (Zahran and Willis 2009). Most of these species were also very abundant in the wettest zone of the Erkwit mist oasis, Sudan (Kassas 1956). Additionally, healthy populations of *Dracaena ombet* were observed at higher elevations on the northern slopes of Gebel Elba (Kamel et al. 2015; Elnoby and Moustafa 2017). *Dracaena ombet* is usually associated with *O. europaea* subsp. *cuspidata* on Gebel Elba, and scattered populations extend southward from Sudan to Somalia along the African hills that face the Red Sea (Marrero et al. 1998; Kamel et al. 2015).

According to White (1983) and Kürschner et al. (2008) the evergreen '*Olea* woodland' is in close association with the *Vachellia-Commiphora* woodland sensu Zohary (1973), which characterize the lower slopes and also to the montane forest communities of *Juniperus procera* forest. Because of the lower topography of Gebel Elba (1435 m), we encountered the *Olea* woodland but not the upper montane *Juniperus procera* woodland which occured above ca. 2000 m in the Asir mountains, Saudi Arabia and the Yemen highlands (Kürschner et al. 2008). Also, the *Dracaena ombet - Olea europaea* subsp. *cuspidata* community here is found at lower elevations (560–680 m) than the community of *Tarchonanthus camphoratus - Olea europaea* subsp. *cuspidata* (1600–2000 m) in the Arabian Peninsula (Kürschner et al. 2008).

Environmental drivers

The water supply for plants strongly depends on soil structure, rainfall, and plant cover. The capacity of soil to store moisture, in turn, depends on the depth and quality of soil supporting plant growth (Körner 2012). Sandy soils at low elevations exhibited poor water storage capacities in our study. The sandy plain mainly supported the growth of drought-tolerant trees, e.g., *Vachellia tortilis* subsp. *tortilis*, *V. tortilis* subsp. *raddiana* and *Balanites aegyptiaca* (Zahran and Willis 2009). However, soils in rocky habitats at higher elevations often have higher water holding capacities. Fine soil material accumulates in rock crevices, and rainwater is well protected against evaporation (Zohary 1973; Deil 2014). The sandy loamy soils support a dense growth of *Olea* trees (Ahmed et al. 2016). Furthermore, water droplets from mist and clouds increase the moisture content of soils and reduce plant transpiration rates (Hegazy and Lovett-Doust 2016). The drought stress has a stronger effect on species richness than physiological stress associated with extreme soil pH values (Palpurina et al. 2017). The elevational gradient of the studied wadis could mirror an inversed stress gradient (Abutaha et al. 2019). In arid climates, water evaporates quickly, leading to an increase in the alkalinity and EC of soil (Knapp 1973; Abutaha 2010). At higher elevations, orographic precipitation decreases the pH and EC. This negative relationship between precipitation and soil pH results in favourable soil conditions for plant growth at higher wadis. Although we did not determine the soil moisture content, orographic precipitation and the soil quality at higher elevations seem to support the growth of moist vegetation.

Plant diversity (species richness)

In the wadi systems of Gebel Elba, the species richness increased from low to mid elevation, followed by a plateau pattern from mid to high elevation (Abutaha et al. 2019). This pattern represented the transition from desert to mountain wadi systems. The increase in species richness was the result of reduced climatic stress and increased water availability. The high species richness from mid to higher elevations was related to more climatically suitable conditions for plant growth and diversity (Ghazanfar 1991; El-Keblawy et al. 2016; Hoppe et al. 2018). However, there are many other factors that may affect plant species richness, particularly mountain topography. A complex topography results in relatively greater habitat diversity. Cliffs, crevices and large boulders offer more favourable conditions to plants (Zohary 1973; Hegazy and Lovett-Doust 2016). For example, rocky habitats collect water run-off, supporting dense tree populations. Furthermore, the topography offers more shade for herbs and shrub species. Plant growth is commonly less constrained by soil moisture shortages at high elevations than at low elevations. Precipitation often increases with increasing elevation, and the evaporation/precipitation ratio decreases (Körner 2007). The increase in richness on Gebel Elba could thus be the result of reduced stress and an increase in water availability due to orographic precipitation at higher elevations (Abutaha et al. 2019).

Deciduous / evergreen trees pattern with elevation

The tree limit in arid mountains is mainly determined by drought resistance (Gieger and Leuschner 2004; Karger et al. 2019). The natural vegetation of Gebel Elba includes deciduous and evergreen woodlands (Zohary 1973). The studied elevational gradient (130–680 m) seems to be a major stress gradient in terms of water availability and temperature. The lower elevations are more arid and thus support the growth of scattered drought-deciduous species such as *Vachellia* trees. However, the orographic precipitation at higher elevations exhibit a trend of increasing evergreen species richness that are less resistant to drought (Zahran and Willis 2009). Hence, we can confirm that deciduous species prevail in the more arid parts of the total elevational gradient and occur

in the upper parts as they also can cope with the humid conditions. Nevertheless, drought-resistant deciduous trees appear to be outcompeted by evergreen species with continuous increasing elevation. Above 500 m, evergreen species continuously dominate the vegetation relevés. This confirms our findings from the vegetation classification, i.e. evergreen *Olea* and *Ficus* communities compared with identified deciduous vegetation units *Vachellia* and *Balanites*. Local tree limits can also be greatly altered by fine-scale topography (Case and Duncan 2014; Karger et al. 2019). Up to 400 m, the slopes of Gebel Elba mainly comprise of open sandy plain or stony habitats. From 500 m upward, the mountain slopes of Wadi Marafai become steeper and narrower, thus providing more shadow, and the rockier slopes increase water runoff to wadi beds (Abutaha et al. 2019).

Conclusion

In this study, we identified seven communities along the elevational gradients of four wadis in the northern slopes of Gebel Elba. These communities show an altitudinal zonation and represent the core of the Eritreo-Arabian (tropical) vegetation in the Gebel Elba National Park, Egypt. Two main woodland types are observed in Gebel Elba; first, a deciduous *Vachellia* woodland, appearing in the desert plain and foothills to the mid-elevations of Gebel Elba (communities III–VII). Second, an evergreen *Olea* woodland, at the upper moisture altitudes (community I). The lower limit of the evergreen vegetation in Gebel Elba is found to be lower than in the higher mountains of East Africa and tropical Arabia. The studied elevational gradient mirrors a typical stress gradient. We found that each plant community within the *Vachellia* woodland is restricted to a definite habitat depending on its ability to adapt to drought stress, while the climatically more favourable habitats are occupied by the *Olea* community. The *Ficus* community (II) represents a transition zone between deciduous and evergreen communities. In sum, orographic precipitation, soil quality and complex topography are the main factors that affect the vegetation structure and species richness of Gebel Elba.

Author contributions

M.M.A. carried out fieldwork and soil analysis, M.M.A. and J.O. performed the statistical analyses and wrote the first draft of the manuscript, while all authors contributed to the final version.

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Appendix 1

Species list including information on growth form and the distribution of species in the studied Wadis (M = Marafai, A = Acow, K = Kansisrob, and Y = Yahmib).

	Family	Species incl. author	Life cycle	Life form	Growth form	Wadi			
						M	A	K	Y
1	*Acanthaceae*	***Barleria hochstetteri*** Nees	P	Ch	shrub	*			
2		***Blepharis edulis*** (Forssk.) Pers.	P	Ch	herb	*	*	*	
3		***Dicliptera paniculata*** (Forssk.) I. Darbysh.	A	Th	herb	*	*	*	
4	*Aizoaceae*	***Aizoon canariense*** L.	A	Th	herb	*	*	*	*
5	*Amaranthaceae*	***Achyranthes aspera*** L. var. ***sicula*** L.	P	H	herb	*		*	
6		***Aerva javanica*** (Burm. f.) Juss. ex Schult. in Roem. & Schult. var ***javanica***	P	Ch	herb	*	*	*	
7		***Aerva lanata*** (L.) Juss. ex Schult.	P	Ch	herb	*	*		
8		***Amaranthus graecizans*** L. subsp. ***aschersonianus*** (Thell.) Costea, D. M. Brenner & Tardif	A	Th	herb	*	*	*	
9		***Chenopodiastrum murale*** (L.) S. Fuentes, Uotila & Borsch	A	Th	herb	*	*	*	*
10		***Psilotrichum gnaphalobryum*** (Hochst.) Schinz	P	Ch	herb	*			
11		***Pupalia lappacea*** (L.) Juss.	P	Ch	herb	*			
12	*Amaryllidaceae*	***Pancratium tortuosum*** Herb.	P	G	herb	*	*	*	
13	*Anacardiaceae*	***Pistacia khinjuk*** Stocks var. ***glabra*** Schweinf. ex Engl.	P	Ph	tree	*			
14		***Searsia flexicaulis*** (Baker) Moffett	P	Ph	tree	*			
15		***Searsia glutinosa*** subsp. ***abyssinica*** (Hochst. ex Oliv.) Moffett	P	Ph	tree	*			
16		***Searsia tripartita*** (Ucria) Moffett	P	Ph	tree	*			
17	*Apiaceae*	***Pimpinella etbaica*** Schweinf.	A	Th	herb	*	*		
18	*Apocynaceae*	***Calotropis procera*** (Aiton) W. T. Aiton	P	Ph	tree		*		*
19		***Carissa spinarum*** L.	P	Ph	shrub/liana	*			
20		***Leptadenia pyrotechnica*** (Forssk.) Decne.	P	Ph	shrub		*		*
21		***Pergularia daemia*** (Forssk.) Chiov.	P	Ch	liana	*			
22		***Periploca aphylla*** Decne. subsp. ***laxiflora*** (Bornm. ex Drar) Browicz	P	Ph	shrub	*	*		
23	*Asparagaceae*	***Dracaena ombet*** Heuglin ex Kotschy & Peyr. subsp. ***ombet***	P	Ph	tree	*			
24	*Asphodelaceae*	***Asphodelus tenuifolius*** Cav.	A	Th	herb	*	*	*	*
25	*Asteraceae*	***Bidens bipinnata*** L.	A	Th	herb	*			
26		***Bidens schimperi*** Sch. Bip. ex Walp.	A	Th	herb	*	*		

	Family	Species incl. author	Life cycle	Life form	Growth form	Wadi			
						M	A	K	Y
27	*Asteraceae*	***Echinops hussonii*** Boiss.	P	H	herb	*	*	*	
28		***Launaea nudicaulis*** (L.) Hook. f.	P	H	herb		*		
29		***Osteospermum vaillantii*** (Decne.) Norl.	P	H	herb	*		*	
30		***Pegolettia senegalensis*** Cass.	A	Th	herb	*	*		
31		***Phagnalon schweinfurthii*** Sch. Bip. ex Schweinf.	P	Ch	herb	*			
32		***Pulicaria petiolaris*** Jaub. & Spach	P	H	herb	*			
33		***Pulicaria undulata*** (L.) C. A. Mey.	P	Ch	shrub	*	*	*	
34		***Reichardia tingitana*** (L.) Roth subsp. ***tingitana***	A	Th	herb	*	*		
35		***Senecio flavus*** (Decne.) Sch. Bip.	A	Th	herb	*			
36		***Urospermum picroides*** (L.) Scop. ex. F. W. Schmidt	A	Th	herb	*	*	*	
37	*Boraginaceae*	***Arnebia hispidissima*** (Sieber ex Lehm.) A. DC.	A	Th	herb		*		
38		***Heliotropium bacciferum*** Forssk.	P	Ch	herb				*
39		***Heliotropium supinum*** L.	A	Th	herb				*
40		***Heliotropium zeylanicum*** (Burm. f.) Lam.	P	Ch	herb	*		*	
41		***Trichodesma africanum*** (L.) R. Br. var. ***africanum***	A	Th	herb	*	*		
42		***Trichodesma ehrenbergii*** Schweinf.	P	H	herb	*	*	*	
43	*Brassicaceae*	***Diceratella elliptica*** (DC.) Jonsell	P	H	herb	*	*		
44		***Farsetia longisiliqua*** Decne.	P	Ch	shrub	*	*	*	
45		***Sisymbrium erysimoides*** Desf.	A	Th	herb	*	*	*	
46	*Burseraceae*	***Commiphora gileadensis*** (L.) C. Chr.	P	Ph	shrub			*	
47	*Capparaceae*	***Boscia senegalensis*** (Pers.) Lam. ex Poir.	P	Ph	shrub	*			
48		***Capparis decidua*** (Forssk.) Edgew.	P	Ph	tree	*		*	
49		***Maerua crassifolia*** Forssk.	P	Ph	tree	*	*	*	*
50		***Maerua oblongifolia*** (Forssk.) A. Rich.	P	Ch	liana			*	
51	*Caryophyllaceae*	***Cometes abyssinica*** R. Br. ex Wall.	A	Th	herb	*	*	*	
52		***Paronychia argentea*** Lam.	A	Th	herb			*	
53		***Spergularia flaccida*** (Madden) I. M. Turner	A	Th	herb	*		*	*
54	*Celastraceae*	***Gymnosporia senegalensis*** (Lam.) Loes.	P	Ph	shrub	*			
55	*Cleomaceae*	***Cleome amblyocarpa*** Barratte & Murb.	A	Th	herb		*		*
56	*Commelinaceae*	***Commelina benghalensis*** L.	A	Th	herb	*	*		
57		***Commelina forskaolii*** Vahl	A	Th	herb	*	*	*	
58	*Convolvulaceae*	***Convolvulus hystrix*** Vahl subsp. ***hystrix***	P	Ch	shrub	*		*	
59		***Cuscuta chinensis*** Lam.	A	Th	liana	*	*	*	
60		***Cuscuta pedicellata*** Ledeb.	A	Th	liana		*		
61		***Ipomoea biflora*** (L.) Pers.	A	Th	herb	*	*	*	
62	*Cucurbitaceae*	***Citrullus colocynthis*** (L.) Schrad.	P	H	herb	*	*	*	
63		***Cucumis prophetarum*** L. subsp. ***dissectus*** (Naudin) C. Jeffrey	P	H	herb	*			
64		***Cucumis prophetarum*** L. subsp. ***prophetarum***	P	H	herb	*	*	*	*
65		***Kedrostis gijef*** (Forssk. ex. J. F. Gmel.) C. Jeffrey	P	Ch	liana	*	*		
66	*Cyperaceae*	***Cyperus laevigatus*** L. subsp. ***laevigatus***	P	H	sedge	*			
67	*Ebenaceae*	***Euclea racemosa*** Murray subsp. ***schimperi*** (A. DC.) F. White	P	Ph	tree	*			
68	*Ephedraceae*	***Ephedra foliata*** Boiss. ex C. A. Mey.	P	Ph	shrub	*	*	*	
69	*Euphorbiaceae*	***Chrozophora oblongifolia*** (Delile) A. Juss. ex Spreng.	P	Ch	herb	*		*	
70		***Chrozophora tinctoria*** (L.) Raf.	A	Th	herb	*	*		
71		***Euphorbia cuneata*** Vahl subsp. ***cuneata***	P	Ph	tree	*	*	*	
72		***Euphorbia nubica*** N. E. Br.	P	Ch	shrub	*	*	*	
73		***Euphorbia granulata*** Forssk.	A	Th	herb	*		*	
74		***Euphorbia*** sp. L.	A	Th	herb			*	
75	*Fabaceae*	***Crotalaria impressa*** Nees ex Walp.	A	Th	herb			*	
76		***Crotalaria senegalensis*** (Pers.) Bacle ex DC.	A	Th	herb			*	
77		***Delonix elata*** (L.) Gamble	P	Ph	tree		*	*	
78		***Indigofera spinosa*** Forssk.	P	Ch	shrub	*	*	*	*
79		***Rhynchosia minima*** (L.) DC. var. ***memnonia*** (Delile) T. Cooke	P	Ch	liana	*			
80		***Senegalia laeta*** (R. Br. ex Benth.) Seigler & Ebinger	P	Ph	tree	*			
81		***Senegalia mellifera*** (Benth.) Seigler & Ebinger	P	Ph	shrub	*	*	*	
82		***Senna italica*** Mill.	P	Ch	herb	*	*	*	*
83		***Tephrosia purpurea*** (L.) Pers. subsp. ***apollinea*** (Delile) Hosni & El-Karemy	P	Ch	herb	*	*	*	*
84		***Vachellia etbaica*** (Schweinf.) Kyal. & Boatwr.	P	Ph	tree	*	*		
85		***Vachellia oerfota*** (Forssk.) Kyal. & Boatwr. var. ***oerfota***	P	Ph	shrub			*	
86		***Vachellia*** sp. Wight & Arn.	P	Ph	tree		*		
87		***Vachellia tortilis*** (Forssk.) Galasso & Banfi subsp. ***raddiana*** (Savi) Kyal. & Boatwr.	P	Ph	tree	*	*	*	*
88		***Vachellia tortilis*** (Forssk.) Galasso & Banfi subsp. ***tortilis***	P	Ph	tree	*	*	*	*
89	*Geraniaceae*	***Erodium neuradifolium*** Delile ex Godr.	A	Th	herb	*	*		
90		***Geranium trilophum*** Boiss.	A	Th	herb	*	*	*	
91	*Lamiaceae*	***Lavandula coronopifolia*** Poir.	P	Ch	shrub	*	*	*	
92		***Leucas neuflizeana*** Courbon	A	Th	herb	*			
93		***Ocimum forskoelei*** Benth.	P	Ch	shrub	*	*		
94		***Otostegia fruticosa*** (Forssk.) Schweinf. ex Penzig subsp. ***fruticosa***	P	Ch	shrub	*	*		
95		***Salvia aegyptiaca*** L.	P	Ch	shrub	*	*		
96	*Loranthaceae*	***Plicosepalus acaciae*** (Zucc.) Wiens & Polhill	P	Ph	shrub	*	*		
97		***Plicosepalus curviflorus*** (Benth. ex Oliv.) Tiegh.	P	Ph	shrub	*	*		
98	*Malvaceae*	***Abutilon bidentatum*** Hochst. ex A. Rich.	P	Ch	shrub	*			
99		***Abutilon fruticosum*** Guill. & Perr.	P	Ch	shrub	*	*	*	
100		***Abutilon pannosum*** (G. Forst.) Schltdl.	P	Ph	shrub	*	*	*	
101		***Grewia tenax*** (Forssk.) Fiori	P	Ph	shrub	*			
102		***Grewia tembensis*** Fresen.	P	Ph	shrub	*			

	Family	Species incl. author	Life cycle	Life form	Growth form	Wadi			
						M	A	K	Y
103	*Malvaceae*	***Grewia villosa*** Willd.	P	Ph	shrub	*			
104		***Hibiscus micranthus*** L. f.	P	Ch	shrub	*	*	*	
105		***Hibiscus vitifolius*** L.	P	Ch	shrub	*	*		
106		***Malva parviflora*** L.	A	Th	herb		*		
107		***Pavonia triloba*** Guill. & Perr.	P	Ch	herb	*			
108		***Triumfetta flavescens*** Hochst. ex A. Rich.	P	Ch	shrub	*	*	*	*
109		***Triumfetta rhomboidea*** Jacq.	P	Ch	shrub	*			
110	*Menispermaceae*	***Cocculus pendulus*** (J. R. & G. Forst.) Diels	P	Ch	liana	*	*	*	*
111	*Moraceae*	***Ficus palmata*** Forssk.	P	Ph	tree		*		
112		***Ficus salicifolia*** Vahl	P	Ph	tree	*	*		
113	*Moringaceae*	***Moringa peregrina*** (Forssk.) Fiori	P	Ph	tree	*	*		
114	*Nyctaginaceae*	***Commicarpus helenae*** (Roem. & Schult.) Meikle	P	Ph	shrub	*		*	
115	*Oleaceae*	***Jasminum fluminense*** Vell. subsp. ***gratissimum*** (Deflers) P. S. Green	P	Ph	liana	*			
116		***Jasminum grandiflorum*** L. subsp. ***floribundum*** (R. Br. ex Fresen.) P. S. Green	P	Ph	liana/shrub	*			
117		***Olea europaea*** L. subsp. ***cuspidata*** (Wall. ex G. Don) Ciferri	P	Ph	tree	*			
118	*Orobanchaceae*	***Lindenbergia indica*** (L.) Vatke	P	Ch	shrub	*	*		
119	*Oxalidaceae*	***Oxalis anthelmintica*** A. Rich.	P	G	herb	*	*		
120	*Phyllanthaceae*	***Andrachne aspera*** Spreng.	P	Ch	herb	*			
121	*Plantaginaceae*	***Nanorrhinum hastatum*** (R. Br. ex Benth.) Ghebr.	A	Th	herb	*	*	*	
122		***Plantago afra*** L.	A	Th	herb	*		*	*
123		***Plantago ciliata*** Desf.	A	Th	herb		*		
124	*Poaceae*	***Brachypodium distachyon*** (L.) P. Beauv.	A	Th	grass		*		*
125		***Bromus fasciculatus*** C. Presl	A	Th	grass	*			
126		***Cenchrus ciliaris*** L.	P	H	grass	*	*	*	*
127		***Cenchrus pennisetiformis*** Hochst. & Steud.	A	Th	grass	*	*	*	*
128		***Cenchrus setiger*** Vahl	P	G	grass			*	
129		***Centropodia forskalii*** (Vahl) Cope	P	H	grass		*		
130		***Cynodon dactylon*** (L.) Pers.	P	G	grass		*	*	
131		***Digitaria nodosa*** Parl.	P	H	grass			*	
132		***Eragrostis cilianensis*** (All.) Vignolo ex Janch.	A	Th	grass	*	*		
133		***Melanocenchris abyssinica*** (R. Br. ex Fresen.) Hochst.	A	Th	grass	*	*		
134		***Panicum turgidum*** Forssk.	P	G	grass	*	*		
135		***Stipagrostis ciliata*** (Desf.) De Winter	P	H	grass			*	
136		***Tragus racemosus*** (L.) All.	A	Th	grass		*		
137		***Urochloa deflexa*** (Schumach.) H. Scholz	A	Th	grass		*	*	
138	*Polygonaceae*	***Rumex simpliciflorus*** Murb.	A	Th	herb	*			
139		***Rumex vesicarius*** L.	A	Th	herb	*	*	*	
140	*Portulacaceae*	***Portulaca oleracea*** L. subsp. ***oleracea***	A	Th	herb	*	*		
141	*Primulaceae*	***Lysimachia arvensis*** (L.) U. Manns & Anderb.	A	Th	herb		*		
142	*Pteridaceae*	***Onychium divaricatum*** (Poir.) Alston	P	H	herb	*			
143	*Resedaceae*	***Caylusea hexagyna*** (Forssk.) M. L. Green	A	Th	herb		*	*	
144		***Ochradenus baccatus*** Delile	P	Ph	shrub	*	*	*	
145	*Rubiaceae*	***Galium spurium*** L.	A	Th	herb	*			
146	*Salvadoraceae*	***Salvadora persica*** L.	P	Ph	shrub	*		*	
147	*Sapindaceae*	***Dodonaea viscosa*** Jacq.	P	Ph	shrub	*			
148	*Scrophulariaceae*	***Scrophularia arguta*** Sol. ex Aiton	A	Th	herb	*	*		
149	*Solanaceae*	***Lycium shawii*** Roem. & Schult.	P	Ph	shrub	*	*	*	*
150		***Solanum forskaolii*** Dunal	P	Ch	shrub	*	*	*	
151		***Solanum incanum*** L.	P	Ch	shrub	*	*		
152		***Solanum nigrum*** L. var. ***elbaensis*** Täckh. & Boulos	A	Th	herb	*	*		
153		***Solanum villosum*** Mill. subsp. ***villosum***	A	Th	herb	*	*		
154		***Withania somnifera*** (L.) Dunal	P	Ch	shrub			*	
155	*Urticaceae*	***Forsskaolea tenacissima*** L.	P	H	herb	*	*	*	*
156		***Forsskaolea viridis*** Webb	A	Th	herb	*	*	*	
157		***Parietaria debilis*** G. Forst.	A	Th	herb	*	*	*	
158	*Verbenaceae*	***Lantana viburnoides*** (Forssk.) Vahl	P	Ch	shrub	*			
159	*Violaceae*	***Viola cinerea*** Boiss. var. ***stocksii*** (Boiss.) Becker	A	Th	herb	*			
160	*Zygophyllaceae*	***Balanites aegyptiaca*** (L.) Delile	P	Ph	tree	*	*	*	*
161		***Tribulus terrestris*** L.	A	Th	herb	*	*	*	
162		***Zygophyllum simplex*** L.	A	Th	herb	*	*	*	*

Supplementary material

Supplementary material 1

Supplementary tables showing the percentage cover and the distribution of perennial species in the studied relevés for each community. Wadi Marafai (M), W. Acow (A), W. Kansisrob (K), and W. Yahmib (Y).

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